

DESERT RODENT ADAPTATION AND COMMUNITY STRUCTURE¹

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ABSTRACT.— Desert rodent communities are compared for evidence of convergent evolution at various levels of organization, including the systemic (physiological, anatomical, etc.), autecological, and synecological. Convergence is quite pronounced at the systemic level, less pronounced at the autecological level, and even less detectable at the synecological level. This is not to imply that community convergence does not occur, but rather that our current abilities to quantify and detect convergence at the community level are rudimentary—and our data base is still far from adequate to the task of rigorously comparing community attributes. Most research on the ecology, behavior, physiology, and community structure of desert rodents has been conducted on North American species inhabiting deserts of the United States. The patterns of species coexistence that have been elucidated in these deserts are often presumed to apply in other deserts of the world. It has become apparent in recent years, however, that the complex North American desert system is unique in many ways, perhaps especially in the biogeographic history of its habitats and faunas, from most of the other deserts of the world. The North American deserts offer an unusually diverse fauna of desert rodents (both alpha and beta diversity are high) which evidences patterns of distribution and coexistence that excite biologists working with the mechanisms of competitive interactions. Similar studies carried out in other deserts might very well lead to a different set of ideas concerning the ways in which desert rodents manage to coexist and how desert communities develop over time. The present paper is an attempt to compare community structure and development as well as patterns of coexistence among the various faunas of desert rodents of the world. Although data are sketchy for many areas, sufficient information is available to allow a preliminary comparison of methods of adaptation and coexistence to be made.

Research on desert rodents began over a century ago in the United States. The earliest studies examining desert rodents were those of Coues (e.g., 1868), Coues and Allen (1877), and C. Hart Merriam and his team of investigators from the old Biological Survey. In addition to the taxonomic investigations of Merriam himself (e.g., Merriam 1889) and those of his subordinates (e.g., Osgood 1900, Goldman 1911, Howell 1938), there were other studies by contemporaries of the survey scientists (e.g., Grinnell 1932, Benson 1933, Blossom 1933, Hall and Dale 1939). After the initial work had formed a rather firm taxonomic foundation, field research entered the stage of natural historical, ecological, and biogeographical studies (e.g., Taylor and Vorhies 1923, Bailey 1931, Benson 1935, Dice and Blossom 1937, Blair 1943, Monson and Kessler 1940, Tappe 1941, Fitch 1948). Although ecological and taxonomic investigations continued during the mid-twentieth century, much research was centered on the physiological adaptations of ro-

dent to arid environments; this research was greatly stimulated by the studies of the Schmidt-Nielsen (see Schmidt-Nielsen 1964, for a review), who showed convincingly that some small mammals were well adapted physiologically to pronounced aridity. Later research has allowed a finer resolution of the mechanisms of physiological adaptation to deserts (e.g., McNab and Morrison 1963, MacMillen 1964a, 1964b, 1972, Hudson 1964a, Chew 1965, Carpenter 1966, Brown 1968, Brown and Bartholomew 1969, Mullen 1971, Abbott 1971, Whitford and Conley 1971, Maxson and Morton 1974, Baudinette 1974).

Within the last 15 years, desert research in the United States has centered on problems dealing with species coexistence. It has long been remarked that the deserts of the United States support a broad diversity of species, but only since the mid-1960s have researchers attempted both to understand the causative agents of this diversity as well as the mechanisms of species coexistence. Earlier

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studies of coexistence had examined the possible roles of abiotic factors on species distribution patterns (e.g., Hardy 1945), but later research has focused on the role of interspecific competition as a possible determinant of distributional patterns (see Brown et al. 1979, for a review). Research emphasis over the last decade has centered on the body sizes of coexisting rodent species (e.g., Brown 1973, Brown 1975, Bowers and Brown 1982), the sizes of seeds taken by granivorous rodents (e.g., Brown and Lieberman 1973, Mares and Williams 1977), the distribution of the seed resource in the desert and whether or not clumped seeds are favored by bipedal species (e.g., Reichman and Oberstein 1977, Wondolleck 1978, Price 1978, Hutto 1978, Trombulack and Kenagy 1980), and on the importance of microhabitat selection in maintaining coexistence (e.g., Rosenzweig 1973, 1977, 1979, Rosenzweig et al. 1975, Schroder and Rosenzweig 1975, Lemen and Rosenzweig 1978).

Each of these areas of research is controversial. For example, Lemen (1978) has strongly criticized the proposed seed size-body size relationship, and support for his position can be garnered from Stamp and Ohmart (1978), M'Closkey (1978), and others. Early indications that bipedal rodents are able to travel greater distances more rapidly and at lower energetic costs than quadrupedal species (e.g., Dawson 1976) have been shown to be in error (Thompson et al. 1980), thus casting doubt on the validity of a linchpin in the theory relating locomotor mode (bipedality) to the habit of foraging on widely dispersed seed clumps (see also Frye and Rosenzweig 1980). Evidence for body size differences among coexisting competitors has been challenged by Conner and Simberloff (1979) and Rebar and Conley (in press). Even the basic premise that competition has helped mold desert rodent communities (Brown 1976, Munger and Brown 1981) has been shown to be a hypothesis that is testable only with the greatest difficulty, if it can be unambiguously tested at all (e.g., Rosenzweig 1981).

The many basic studies done in the arid portions of the United States have made this region one of the best studied areas on earth.

Since ecologists tend to extrapolate the results of research carried on in one biome to other areas supporting apparently similar ecosystems, it is tempting to believe that as we explain patterns of coexistence or adaptation within the deserts of the United States we will have described these patterns for deserts around the world. As MacArthur (1972:1) noted, "To do science is to search for repeated patterns." In this brief essay I will characterize the patterns of adaptation of desert rodents that have been described largely within the conterminous United States. Realizing full well that "natural selection depends for its effectiveness on a series of chances" (Leigh 1971:221), I believe it is important to distinguish between local patterns and those of a global nature. Perhaps all important questions regarding life in deserts can be answered by studying intensively one particular geographic unit—then again, perhaps not. If all deserts are not equal, a very real problem develops in discovering which patterns are truly generalizable.

THE PATTERNS

The first problem that presents itself is that of scale—does one seek patterns at the level of biochemical reactions, organ systems, or communities? The second problem is that of confounding causation. Does bipedality develop, for example, because of intrinsic problems related to integrated locomotor design (e.g., Alexander 1975), or do such seemingly unrelated factors as seed distributions, granivory, predator avoidance, and substrate all play a part in the selection of a particular type of movement? Although it is easy to become overwhelmed by the complexity of desert rodent adaptations, I will limit my analysis to characteristics above the purely biochemical level. This broad brush approach will give an overview of adaptations of desert rodents from the United States and will compare these with rodents from other parts of the world that have also successfully made the transition to desert life. I will in essence be assessing the available literature on desert rodent biology for examples of convergence, "the strongest sort of evidence for the efficacy of selection and for its adaptive orientation of evolution" (Simpson 1953:171).

PHYSIOLOGICAL ADAPTATIONS

Water Balance—North America

Perhaps one of the most widely known traits of small mammals in desert regions is the ability to withstand water deprivation. Schmidt-Nielsen (1964) has provided the most complete summary of the complex adaptations associated with this ability in North American rodents (see also Schmidt-Nielsen 1975, for a discussion of the mechanisms of water conservation in desert rodents). It is clear that withstanding either low free environmental water or high solute loads demands numerous physiological and anatomical specializations. Certainly, the North American Heteromyidae, kangaroo rats and pocket mice, are the most specialized rodents in this regard in the deserts of the United States. Their adaptations include specialized kidneys, elongated renal papillae, long nasal passages for countercurrent heat exchange, and numerous other characteristics that minimize water loss or increase their ability to obtain vegetational water (e.g., Schmidt-Nielsen 1964, Mullen 1971, Kenagy 1973a, Soholt 1975). Similar adaptations, although perhaps not as pronounced, are known to occur in North American cricetines (e.g., Abbott 1971, Andersen 1973), and sciurids (e.g., Hudson 1962, Maxson and Morton 1974). In all these higher taxa, some species are capable of producing fairly concentrated urine, reducing fecal and respiratory water loss, and existing on minimal inputs of free or vegetational water. There is little doubt that the physiological and anatomical adaptations of desert rodents that minimize water loss encompass all the major systems of the organism. For example, Hatton et al. (1972) showed that in desert rodents the cells of that portion of the brain responsible for producing vasopressin (ADH) are multinucleate, a trait that is uncommon in rodents from moist habitats; this trait is very likely related to water retention ability. They examined several species from both New and Old World deserts.

As physiological studies are extended to the arid portions of Mexico, numerous other species will probably be found to be highly adapted for existing in an environment having minimal moisture available for ingestion.

Not all rodents inhabiting North American arid areas are desert specialists (e.g., Lee 1963, Andersen 1973, MacMillen and Christopher 1975). Although it is clear that the ability to withstand water deprivation has a strong phylogenetic component (e.g., Hudson and Rummel 1966, Fleming 1977), it can develop readily in species inhabiting non-desertic habitats where water is scarce (e.g., Fislser 1963, MacMillen 1964b).

Water Balance—Other Deserts

Because of the widespread nature of various physiological adaptations among species of the North American fauna, one might expect that similar types of adaptations would develop in other deserts. Despite the complexity of the suite of traits associated with water independence, this does not appear to be a particularly difficult path for evolution to follow. Indeed, water independence has developed among one or more species of rodents from deserts in Australia (e.g., MacMillen and Lee 1969, Baudinette 1972), Asia (Winkelman and Getz 1962), India (e.g., Ghosh 1975), North Africa (e.g., Burns 1956, Kirmiz 1962 for *Jaculus*, but see Ghobrial and Nour 1975), southern Africa (e.g., Christian 1978, 1979), and Peru (Koford 1968). The extensive Monte Desert of Argentina lacks water-independent species, although *Eligmodontia typus*, a cricetine, is well adapted to process high concentrations of sodium chloride (Mares 1977a). Curiously, although Mares (1977b) did encounter a water independent rodent in Argentina (*Calomys musculus*), it was an inhabitant of the mesic fringes of the desert.

Only a relatively small percentage of the desert rodents of the world has been examined physiologically. Similar adaptations may have developed repeatedly in all deserts of the world. There is some question as to how physiologically specialized the dipodids are (Ghobrial and Nour 1975), but there is little doubt that pronounced adaptations toward aridity have occurred in such disparate families as the Muridae, Dipodidae, Heteromyidae, and Sciuridae. Similar adaptations will probably be found in other families of desert rodents (e.g., Octodontidae, Ctenodactylidae).

The apparent regularity with which physiological adaptations develop is illustrated by their being characteristic not only of granivorous or herbivorous rodents, but of insectivorous-carnivorous rodents (e.g., Whitford and Conley 1971) and small marsupials (e.g., Schmidt-Nielsen and Newsome 1962, MacFarlane 1975, Morton 1980).

Mares (1975a, b, 1976, 1977c) found that not all rodents inhabiting the Monte Desert of Argentina showed pronounced levels of physiological adaptation (see also Meserve 1978). Many species inhabit that region by limiting their activities to relatively mesic microhabitats. In view of the widespread nature of physiological adaptation toward a xeric existence, Mares (1975a, 1976) hypothesized that most of the rodents of the Monte Desert had not reached the region until latest Pliocene, or even Pleistocene, times. Thus, there had not been sufficient time to evolve the complex group of physiological, anatomical, behavioral, and ecological attributes characteristic of desert life.

Although much work remains to be done on the comparative physiology of desert rodents, pronounced convergence and parallelism have occurred in all deserts as the result of similar regimens of natural selection acting on the colonizing stocks of rodents, regardless of their phylogenetic affinities. This convergence (or parallelism, in some cases) extends to many aspects of the behavioral-physiological-anatomical complex involved in osmotic balance. Similarities are seen in the structure of kidneys (e.g., Hudson 1962, Schmidt-Nielsen 1964, MacMillen and Lee 1969, Abdallah and Tawfik 1969, Fleming 1977), in their urine concentrating abilities, in the ability of the animals to withstand desiccation or elevated solute loads, in the elongated nasal passages for heat exchange (this characteristic is in need of comparative studies), and in reduced fecal water loss. Only a few studies have been done examining other avenues of water loss in desert rodents and the adaptations that have evolved to minimize these losses. For example, Kooymann (1963) shows that *Dipodomys merriami* produces a very concentrated milk (thus minimizing lactational water loss). Working with native Australian rodents (*Notomys*, *Pseudomys*), Baverstock et al. (1976) found that

these species did not produce exceptionally concentrated milk. A later study to examine whether or not these rodents actually reduced the amount of milk produced during lactation (and thereby reduced water loss) was inconclusive (Baverstock and Elhay 1979). What is really needed is a broadscale study designed to examine all avenues of water loss and to compare these across taxa. Emphasis should be placed initially on genera that are known desert specialists (e.g., *Dipodomys*, *Microdipodops*, *Perognathus*, *Gerbillus*, *Gerbillurus*, *Desmodillus*, *Meriones*, *Dipus*, *Jaculus*, *Allactaga*, etc.), rather than on species that inhabit only the climatic peripheries of deserts. Extreme adaptations will be more easily detected than will the fine shadings of "average" adaptations that have been modified to allow persistence only at the environmental peripheries of deserts.

Other Physiological Adaptations

Various secretory glands are known in desert rodents (e.g., *Meriones* from India, Wallace et al. 1973; *Notomys* from Australia, Watts 1975), but their function is not clear. The products of sebaceous glands in *Dipodomys* may function as other than secretions to aid in the care of the pelage (Quay 1953). Whether or not such glands are widespread among other taxa of desert rodents is unknown, but a comparative assessment of these structures could prove useful toward understanding their function. Eisenberg (1963, 1975) discusses possible olfactory communication in desert rodents, an area of research essentially unexplored in mammals, particularly desert rodents.

Several species of desert rodents in the United States are known to undergo facultative torpor: these species include cricetine rodents, heteromyids, and sciurids (e.g., Hudson 1964, 1967, Tucker 1966, Chew et al. 1967, Brown and Bartholomew 1969, Kenagy 1973b, Reichman and Van De Graff 1973, Reichman and Brown 1979). Presumably such a strategy allows a rodent to remain inactive during periods of resource scarcity; however, periodic torpor is not limited to rodents from xeric habitats (e.g., Hill 1977). It has been hypothesized that desert rodents have a lower metabolic rate (irrespective of torpor) than

species from mesic habitats (e.g., McNab and Morrison 1963). Hayward (1965) questioned this idea, suggesting that stored fat reserves of laboratory animals had led to artificially low metabolic rates. McNab (1968), however, showed that lower metabolic rates for species from xeric habitats (i.e., a North American cricetine, *Peromyscus crinitus*, and the naked mole rat of Africa [*Heterocephalus glaber*], a bathyergid) characterized individuals whose body fat levels were well within normal limits. Yousef and Johnson (1975) found a correlation between the lower metabolic rate of various North American desert rodent species (representing three families) and reduced thyroxine secretion rate, suggesting a relationship between thyroid activity and metabolic rate; species from xeric areas had significantly lower rates of thyroid activity than species from mesic habitats.

Energy metabolism in North American desert rodents has been examined in both the laboratory (e.g., Dawson 1955, Yousef et al. 1970) and in the field (e.g., Mullen 1971, Soholt 1973, Kenagy 1973b). There are very few comparative studies available on rodents from other deserts (e.g., Dawson 1976, Thompson et al. 1980).

The fact that many similar adaptations are common among species of the three families of rodents inhabiting North American deserts would lead one to speculate that similar traits might be expected in other faunas. All information to date supports the idea that similar physiological strategies toward aridity have evolved independently and repeatedly throughout the world.

ANATOMICAL ADAPTATIONS

North America

Like physiological adaptations, anatomical specializations for desert life are essentially limitless—depending on one's scale, anatomy can be viewed from the cell to the whole organism. Obviously, an organism evolves as an integrated unit. Thus, viewing any structural specialization without regard to its association with function lends a certain artificiality to the analysis. For example, the supraoptic nuclei described above (Hutton et al. 1972) are cellular specializations leading

to gross modifications in brain tissue. These structures play a role in ADH secretion and thereby affect osmotic balance. Nevertheless, from the viewpoint of convergent evolution, it is interesting to know whether similar structures have developed and whether or not they function in similar ways. It is also instructive to learn that similar functions are performed by dissimilar structural adaptations.

Bipedality

Quite often, the term "desert rodent" connotes the genus *Dipodomys*. Much research has centered on species of *Dipodomys*, and kangaroo rats are almost synonymous with "desert adaptation." Nevertheless, kangaroo rats are but one of many genera inhabiting North American deserts. It is probably because of the familiarity of many scientists with *Dipodomys* that most desert rodents are assumed to mirror the adaptations characteristic of that single genus.

Dipodomys are saltatorial and bipedal; they are also granivorous. Because of the association between bipedality and granivory in *Dipodomys*, a causal link between these characteristics has been suggested (e.g., Reichman and Oberstein 1977). It is instructive therefore to examine bipedality in some detail.

Several anatomical studies have examined bipedality in desert rodents (e.g., Hatt 1932, Howell 1932, Klingener 1964, Pinkham 1971, Kaup 1976, Berman 1979). The most extensive study was that of Berman (1979), who compared hind limb osteology and myology in a broad spectrum of desert rodents of the world. She noted that bipedal saltation has arisen independently in five families of rodents: four of these (Heteromyidae, Dipodidae, Pedetidae, and Muridae) have their bipedal species essentially restricted to xeric habitats, whereas the Zapodidae are forest species. Small bipedal saltators have also arisen among extant and extinct marsupials. Berman's analyses led her to conclude that there has been a striking convergence in major musculoskeletal modifications of the hind limb of desert rodents. Similarities in structure are so pronounced that unrelated bipedal species were generally grouped more

closely in multivariate space than were bipedal and quadrupedal members of the same families. Her analyses also showed that there were numerous significant differences among desert rodents in the ways in which bipedality had been achieved—different muscles were elongated or shortened, different mechanical advantages had evolved, and different modifications characterized the feet.

Mares (1980) examined the majority of desert rodent genera in a multivariate analysis of morphoecological characteristics. He noted that bipedality in North American deserts is restricted to granivores (although many obligate granivores in North America are quadrupedal), but when all desert rodents are examined, the supposed link between bipedality and seed eating is not found. There are bipedal granivores (e.g., *Dipodomys*, *Cardiocranius*, *Stylodipus*, some *Jaculus*), bipedal herbivores feeding on above-ground plant parts (e.g., *Pedetes*, which also feed in below-ground plant parts, *Pygeretmus*, *Allactagulus*, some *Allactaga*); bipedal herbivores feeding on below-ground plant parts (some *Allactaga*, some *Jaculus*), bipedal herbivores eating all plant parts (e.g., some *Allactaga*, some *Jaculus*, *Dipus*, *Paradipus*); bipedal omnivores (some *Allactaga*, *Notomys*); and bipedal insectivores (*Salpingotus*, the marsupial *Antechinomys*). In Old World deserts, most obligate granivores are quadrupedal (e.g., *Meriones*, *Gerbillus*, *Tatera*, *Phodopus*, *Brachiones*, *Sekeetamys*, etc.). [Information on the diets of the various genera can be found in Lobachev and Khamdamova (1972), Naumov and Lobachev (1975), Happold (1975), Prakash (1975), Watts (1977), and Wassif and Soliman (1979).]

Thus, bipedality, when viewed on a global scale, appears to have little relation to diet; bipedal species fill all major trophic categories. Although research limited to North American desert species might be interpreted as supporting a link between diet and locomotion, I find no evidence to support this hypothesis in other deserts.

In addition to elongated hind limbs, bipedal rodents have shortened forelimbs, prompting suggestions that the freeing of the forelimbs for stuffing food into the cheek pouches was the primary selective force leading to bipedality (Bartholomew and Carey

1954). In view of the large number of bipedal rodents that lack cheek pouches (including all pedetids, dipodids, and zapodids), the many quadrupedal species that have internal cheek pouches (e.g., cricetids, sciurids, etc.), and the presence of cheek pouches in fossorial geomyids and quadrupedal *Perognathus*, *Liomys*, and *Heteromys*, there is little compelling support for this hypothesis.

One hypothesis that has been invoked to explain bipedality (although it has been tied to the pattern of seed distribution) is differential microhabitat utilization. There is some evidence that bipedal species forage in open areas more frequently than they do under shrubs (e.g., Rosenzweig and Winakur 1969, Brown and Lieberman 1973, Rosenzweig 1973, Brown 1975, Price 1978, Wondolleck 1978); this observation appears to hold for Old World desert species as well (e.g., Naumov and Lobachev 1975), although rigorous quantification of this pattern is needed for all deserts, particularly those of the Old World. Nevertheless, if foraging in open areas is correlated with bipedality, then it is inferential evidence that predator avoidance is a primary selective factor of locomotor mode. This is an old idea (e.g., Howell 1932) that has been restated repeatedly (e.g., Eisenberg 1975, Berman 1979, Mares 1980), but appears to have merit. There is little doubt that predation is an important factor in sparse desert habitats—evolutionarily opting to forage in open microhabitats very likely forces rodents into an entirely new adaptive mode, that of bipedality.

Bipedality is also associated with other anatomical adaptations for predator avoidance (although some of these occur in quadrupedal desert species as well). Enlarged bullae (e.g., Howell 1932, Webster 1962, Lay 1972) or elongated pinnae (e.g., Howell 1932, Eisenberg 1975) are probably adaptations for predator detection (e.g., Legioux and Wisner 1955, Lay 1974). While it might be supposed that the pinnae function in thermoregulation, as is the case in *Lepus* (Hill and Veghte 1976), in fact, the large pinnae of *Allactaga* are not well vascularized and do not function in heat loss (Hill et al. 1974). Bullar hypertrophy is common in desert rodents throughout the world and in other mammals as well

(e.g., Roig 1969, 1972). Fitzwater and Prakash (1969) described *Meriones* in India responding to the wingbeats of avian predators by escaping into burrows.

Finally, desert rodents are generally very pale colored, usually matching the desert soils (e.g., Harrison 1975, Mares 1976, Cloudsley-Thompson 1979). Most authors concur that cryptic coloration is a response to visual predators (cf., Kaufman 1974). Some bipedal species possess a conspicuous black and white tuft on the tip of the tail (almost all bipeds have long tails with a terminal tuft). Tail tufts often regenerate if the tail has been injured (Howell 1932), and it is likely that the tuft itself functions as a rudder that allows the animal to turn abruptly in midair, particularly since the wind resistance of the tuft acts at the end of a long lever arm. The white tail tuft may well act as a flag to confuse or distract predators during their pursuit and/or as a target for predator attack, thus limiting an attack to a tail that may break quite easily and allow the rodent to escape.

An examination of the morphology of desert rodents leads to the conclusion that convergent evolution of structures that reduce the probability of predation is a major evolutionary force.

BEHAVIORAL AND AUTECOLOGICAL ADAPTATIONS

Behavior

Eisenberg (1975) has done the most comprehensive comparative behavioral work with desert rodents. Most are nocturnal; most live in burrows that are plugged during the day. There are many differences among species in aspects of social behavior, but many species in disjunct deserts have remarkably similar behavioral patterns. Unfortunately, little quantitative behavioral research has been done on other than North American species, and even these have been studied primarily in the laboratory. Studies on Old World species include Nel (1975), Daly and Daly (1975a, b), and Agren (1979).

Some workers have examined activity patterns of desert rodents (e.g., Schwab 1966, Jahoda 1973, Kenagy 1973b, 1976, Lockard and Owings 1974, Rosenzweig 1974, French

1975, Lockard 1978). Data from the Old World are in accord with these observations (Naumov and Lobachev 1975). Generally, most desert species are nocturnal (especially bipedal species), although each desert has one or more species of diurnal rodents (usually these are herbivores, Mares 1980).

Autecology

Smith and Jorgensen (1975) and Conley et al. (1977) review reproductive patterns in North American desert rodents, and French et al. (1975) and Wagner (1981) review demographic patterns of desert species throughout the world. Heteromyids generally have small litters, relatively long life spans, low densities, and reproduce during moist and warm times of the year. A complete review of desert rodent reproduction that includes species from each desert has not been produced. In addition to the above reviews, there is some general information available on reproduction for the following areas: Australia (Smith et al. 1972, Crichton 1974, Watts 1979, Aslin and Watts 1980); USSR (Naumov and Lobachev 1975); North Africa (Poulet 1972, 1978, Khammar et al. 1975, Happold 1975, Ghobrial and Nour 1975, Amirat et al. 1977); southern Africa (Nel 1978, Christian 1979, 1980, Butynski 1979); Iran (Lay 1967, Misonne 1975); India (Prakash 1975); Pakistan (Beg et al. 1977); Chile (Fulk 1975).

Although demography has been studied in some detail in North American desert rodents (see above citations), there have been few extensive demographic studies in either South American deserts or in the Old World. Most of these can be located using those citations referring to reproductive patterns (see also Pearson and Ralph, 1978, for Peru).

Synecology

Perhaps the most exciting area of desert ecology today is that dealing with species interactions and community organization. Brown et al. (1979) and Mares (1980) review much of this literature. Research done in North America would suggest that deserts support elevated levels of both species richness and abundance. However, Mares (1979)

has argued that the deserts of the United States support an unusually high diversity of species due to their unique Pleistocene history of refugial formation wherein allopatric speciation processes were amplified. High relative abundance of rodents in U.S. deserts is probably related to the elevated rainfall characterizing much of the North American desert system (e.g., Brown et al. 1979). Much U.S. desert research has been conducted in the Sonoran Desert of southern Arizona, a region that some consider a semidesert due to its relatively high precipitation (e.g., Eisenberg 1975). This preponderance of research in an extremely productive area may have led to a fairly common belief that deserts often support many small mammals. Actually, most deserts seem to support few species of desert rodents at fairly low levels of abundance (e.g., Mares 1976, 1980, Pearson and Ralph 1978, Morton 1979, Brown 1980, Christian 1980), although some areas seem to be equally as rich in species as portions of the U.S. desert system (e.g., Nel 1978).

Just how desert species manage to coexist is the major area of research at the moment, with competition assumed to be a primary selective force leading to observed patterns of microhabitat selection (Rosenzweig 1979), body size differences (Bowers and Brown 1982), or differential utilization of the seed resource (e.g., Reichman and Oberstein 1977). Little comparative work that might shed light on current controversial points has been done in deserts outside the United States, but certainly habitat specificity is a well-known factor characterizing small mammal communities (e.g., Hubert et al. 1977). Nevertheless, Pearson and Ralph (1978:75) found that small mammal species richness in several desert habitats in Peru could be explained by "evolutionary and zoogeographical accident," rather than habitat selection differences.

One reason that controversy surrounds coexistence studies in deserts is that most research to date has been descriptive and inferential. Studies dealing with seed selectivity by rodents have had to contend with the enormous variability in background seed levels and the methodological difficulties of sampling the seed resource (e.g., Brown et al. 1979). Nevertheless, recent trends have fo-

cused on manipulative field experiments (particularly the work of Rosenzweig, Brown, Reichman, and their associates, see above citations). Unfortunately, there has been no parallel movement in experimental research in deserts outside of the United States (or even outside the Sonoran Desert). Theory has far outstripped our empirical data base in desert ecology and experimental data are only beginning to be applied to the many hypotheses that currently abound in the literature.

Recent studies dealing with competition between distantly related taxa promise exciting results if they can be replicated in other deserts (e.g., Brown 1976, Brown and Davidson 1977, Davidson et al. 1980). Mares and Rosenzweig (1978) have done comparative work on this topic and found different patterns in North and South American deserts—they offer an evolutionary explanation for different strategies of granivory in distantly related taxa.

Perhaps the area of research that has been most neglected is that of comparative faunal studies. Mares (1975, 1976, 1980), MacMahon (1976), Mares et al. (1977a, b), Mares and Hulse (1977), Pearson and Ralph (1978), and Morton (1979) have attempted to compare quantitatively diverse desert rodent assemblages. Unfortunately, such studies are hampered by a paucity of data for deserts outside of the United States. As data accrue from current desert research, and as statistical and computational techniques are refined, there should be a great deal of information forthcoming on the ways in which desert rodent communities assemble over time.

CLOSING COMMENTS

If one were to go into an unknown desert region, there are many predictions that could be made concerning the small mammal fauna (particularly the rodent fauna) of the area. Beginning at the most basic levels (anatomy and physiology), we could say that at least some rodents inhabiting the area would exhibit the following adaptations: specialized kidneys (with elongated renal papillae and micro- and macroscopic morphological adaptations) able to concentrate the urine and perhaps process high electrolyte loads; a

counter-current heat exchange system in the nasal region; modified brain cells responsible for ADH secretion; lowered metabolic rate; facultative torpor; ability to exist without free water; minimization of water loss through respiratory, excretory, and defecatory pathways; inflated tympanic bullae or elongated pinnae; bipedality (some species)—with foreshortened forelimbs, long tails, concentrations of muscle mass in proximal limb regions, smaller mechanical advantages for hind limb muscles, elongated distal limb segments, toe reduction, terminal tuft of hair on the tail (often colored black and white); sebaceous glands would be present—sand bathing would be common; dorsal coloration would match the background (pale colors predominating) and countershading would be pronounced; species living on sand would have extremely hirsute hind feet; eyes would be placed dorsally; vibrissae would be abundant and long; white flank markings would be common in bipedal species. There are many other physiological and anatomical traits that would very likely characterize the rodents of this unexplored desert.

Above the systemic level, we could predict the possession of numerous autecological traits: nocturnality would predominate (particularly in bipedal species); both diurnal and nocturnal species would inhabit burrows—these would be plugged during hot periods; bipedal species would differentially forage in open microhabitats, and quadrupedal species would favor closed microhabitats; bipedal forms would occur in flat areas having few rocks; reproduction would be associated with the rainy season, with birth taking place after the rains—populations would peak at this time; territoriality would be pronounced; home ranges would be relatively large; survivorship would be high and fecundity low (e.g., French et al. 1975); population levels would generally be low (although they are often quite high in North American deserts).

Clearly, at the levels of organization from population down to cell, there are numerous predictions that could be made regarding the suite of desert adaptations that would characterize our unknown species, and the lists presented are far from exhaustive. As our level of understanding is refined, more and more

similarities in adaptive strategies become evident.

At the community level, however, our predictions become more tenuous. Our hypothetical desert would probably possess a bipedal and/or a quadrupedal granivore; a micro-omnivore; a medium (squirrel)-sized diurnal omnivore; a small insectivore; a bipedal or a fossorial medium-sized herbivore eating below-ground plant parts; and a larger herbivore (rabbit size). Species richness would be low (although high species richness would not be surprising, particularly if the biogeographic history indicated a multiple-refugial system). Bipedality could occur in all trophic categories except the completely fossorial niche. Coexisting species might exhibit regular patterns of body size differences, and microhabitat selection might be the primary mechanism maintaining coexistence. Granivorous rodents might show inverse relationships in abundance and diversity to the abundance and diversity of other granivores, such as ants or birds. Ants and rodents might be mutualistic over evolutionary time; thus, a lack of mammalian seed predators could prove detrimental to ant seed predators.

There is some controversy as to whether or not there is convergence at the community level (Schall and Pianka 1978). Certainly community studies based in morphometrics will have a proportion of their overall similarity explained by morphological convergence. However, since morphology often reflects function, there is strong evidence that pronounced convergence exists above the systemic level of organization. It is equally clear, however, that strong community convergence is yet to be demonstrated when only ecological parameters are utilized in the faunal comparisons. This is not to say that such convergent evolution does not exist, but rather that the influence of history on faunal development and our inability to quantify rigorously the many ecological attributes of a fauna (and to produce highly predictive and quantitative theories) have not yet allowed us to assess the presence or absence of community convergence. Our best work is yet to be done. The complexity of the seemingly simple desert ecosystem has not yielded to inferential science—the ability of experimental science to clarify the many remaining enigmas is yet to be tested.

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